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Comparison of Invasive and Non-Invasive Techniques for Measuring Fiddler Crab Density in a Salt Marsh

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A COMPARISON OF INVASIVE AND NON-INVASIVE TECHNIQUES FOR MEASURING FIDDLER CRAB DENSITY IN A SALT MARSH

by

Charles R. Hubbard

(Under the direction of Sophie S. George)

ABSTRACT

Quantifying the density of burrowing crabs is challenging, and several techniques have been developed to accomplish it, including burrow counting, visual surveys of surface-active crabs, and substrate excavation. These techniques have been compared in mangrove forests but not in a salt marsh, nor has anyone attempted to excavate traps repeatedly for multiple days. Previous comparisons have not examined these techniques over the course of several months, nor considered the cost and precision associated with each technique. Therefore, from May of 2007 to April 2008, I conducted burrow, visual, single excavation, and repeated excavation surveys to estimate *Uca pugnax* density in a salt marsh on Tybee Island, Georgia and estimated the cost and precision associated with each technique. Only single and repeated excavation accurately measured juvenile density, but these methods were more costly and caused temporary habitat damage. Burrow surveys yielded reliable adult density but visual surveys underestimated adult and juvenile density, likely due to the difficulty of spotting small crabs in thick vegetation. This information may be useful to management officials monitoring fiddler crab populations and their predators in salt marsh ecosystems.

INDEX WORDS: Fiddler crabs, Population density, Salt marsh, Survey techniques

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by

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INTRODUCTION

The salt marsh is one of the most productive ecosystems on earth and serves many important ecological roles in coastal estuarine systems, including wildlife habitat, nursery grounds, water filtering, and storm buffering (Bertness et al. 2003). However, frequent abuse has lead to a loss of more that half of these ecosystems in the United States (Silliman et al. 2005). Furthermore, increasingly frequent tropical storms and rising sea level associated with global warming are expected to cause drastic changes in the ecology of coastal wetlands in the near future (Michener et al. 1997). Perhaps the most important and abundant macrofaunal organisms in salt marshes are fiddler crabs of the genus *Uca* (Class Ocypodidae) (Teal 1958). Their burrows increase the circulation of oxygen and nutrients in the substrate, which greatly improves primary production (Bertness 1985). *Uca spp.* consume large quantities of organic debris and in turn become an important source of food for other animals (Grimes et al. 1989).

Due to their importance in estuarine systems, choosing the best survey technique to quantify the relative abundance of fiddler crabs is a critical issue to research biologists and coastal managers. A number of techniques have been developed, including non-invasive techniques such as burrow counting (Kerwin 1971, Mouton and Felder 1996) and visual surveys of surface active crabs (Golley et al. 1962, Nobbs and McGuinness 1999), as well as invasive techniques such as substrate excavation (Teal 1958, Miller and Maurer 1973), capture-recapture surveys (Hockett and Kritzler 1972), and pitfall trapping (Salmon and Hyatt 1983). Burrow and visual surveys are common despite growing evidence of their unreliability (Backwell et al. 1998). For example, comparison studies of Ocypodid survey techniques have been conducted recently in the mangrove forests of

East Africa (Macia et al. 2001, Skov and Hartnoll 2001) and Australia (Nobbs and McGuinness 1999), as well as the coastal mudflats of Portugal (Jordao and Oliveira 2003). Burrow surveys yielded reliable estimates of resident size (Lourenco et al. 2000, Skov and Hartnoll 2001, Daleo et al. 2003), but cannot reveal the sex of resident crabs and have often overestimated density when compared to substrate excavation (Macia et al. 2001, Jordao and Oliveira 2003). Visual surveys can be used to quantify sex ratio (Nobbs and McGuinness 1999) but cannot measure size distribution and have often underestimated density, especially in thick vegetation (Lourenco et al. 2000, Skov and Hartnoll 2001). Substrate excavation accurately estimates density, but it has been criticized because of its damage to the habitat and the labor involved (Lourenco et al. 2000, Macia et al. 2001). These techniques have not been compared in a salt marsh or over the course of several months. No attempt has been made to excavate plots repeatedly over the course of several days or examine the cost or precision associated with fiddler survey techniques.

The purpose of the following study was to compare burrow, visual, single excavation, and repeated excavation surveys of *Uca pugnax* in a U.S. salt marsh over the course of multiple months. I compared ….

I. the efficiency of each technique for estimating crab density, by conducting
    a. all four techniques on the same plots.
    b. non-invasive surveys and single excavation on different plots.

II. the cost and precision associated with each survey technique.

Based on previous comparisons, I expected burrow surveys to yield the highest densities, followed by repeated and single excavation, and visual surveys to yield the lowest densities in all cases because of the difficulty of spotting crabs in thick vegetation and of spotting juveniles at a distance. Based upon previous experience with this site, I expected juveniles to be more abundant than adults. I expected invasive techniques to be more costly than non-invasive techniques in terms of time, money, and habitat damage.

METHODS

I. Comparing the efficiency of survey techniques for estimating crab density.

I conducted the following study in a *Spartina alterniflora* marsh on Tybee Island, Georgia (Figures 1 and 2). The site (32°00'49N and 80°52'52W) is flooded twice daily by Lazaretto Creek. During each visit, I recorded substrate salinity (34 to 48 ppt), pH (6.6-7.9), and temperature (19-37 ºC). I counted *Uca pugnax*, a common resident of salt marshes from Massachusetts to Florida (Teal 1958), along three transect lines in a 30X60m area (Figure 3). Plots used in all comparisons were haphazardly stratified along these transect lines. In some comparisons, I conducted techniques on the same plots, whereas in others, techniques were conducted on different plots. Far more plots could be surveyed by non-invasive techniques when single excavations were conducted on a separate plot set. However, a more powerful statistical analysis could be used when all techniques were conducted on the same plots.

In all surveys, I distinguished adults as those crabs or burrows that were greater than 9 mm in width. I measured burrow apertures with a plastic ruler but had to estimate the size of crabs in visual surveys. I measured the carapace width of all crabs counted in excavation surveys with vernier calipers. A total of 2877 crabs were measured in 6 months of surveys.

(a) Comparing non-invasive (burrow and visual) and invasive (single and repeated excavation) survey techniques

To compare the efficiency of two non-invasive (burrow and visual) and two invasive (single and repeated excavation) fiddler crab survey techniques for estimating total, adult, and juvenile *U. pugnax* density, I conducted all surveys on a set of 15 plots in

December 2007 and another set in April 2008. I haphazardly distributed orange flags along each of three transect lines and counted all crabs visible on the surface within 30 cm each flag with Audubon 8.5X44mm binoculars. At the next diurnal high tide, I placed cylindrical plastic traps over each flag and hammered those traps 10 cm into the substrate. These traps were made from 208 L plastic chemical drums. Each device measured 60cm in diameter and 30cm in height and had a metal strap fastened to the base as a cutting edge (Figure 4). When the tide receded, I counted all burrows within each trap. I excavated the same plots for 10 min each day for 4 days. All crabs that could be handled and counted within the given time frame were released outside the trap. The first day was considered a single excavation survey and all four days were included in the repeated excavation analysis.

I used model-1, two-way ANOVAs to test the effects of all four techniques and month (fixed factors) on total, adult, male, female, and juvenile *U. pugnax* density. I also used model-I, two-way ANOVAs to test the effects of sampling day and month (fixed factors) on total, male, female, and juvenile *U. pugnax* density measured by repeated excavation. I also tested the interaction between sampling day and month. All data were square root transformed for analysis and assumptions of parametric tests were satisfied. All analyses were run using JMP™ software.

(b) Comparing non-invasive (burrow and visual) and single excavation survey techniques

To compare the efficiency of burrow and visual survey techniques for estimating total, adult, and juvenile *U. pugnax* density, I distributed 45 permanent 50X50-cm plots within the 60X30m study area described above (Figure 3). I marked the corners of each plot with 10cm PVC posts and recorded their coordinates with a global positioning device. Surveys were conducted once a month from May to November 2007 (excluding October) and fieldwork was initiated 2 hours before low tide. I counted surface-active crabs from a distance of 3m using Audubon 8.5X44mm binoculars and burrows at the plots.

I used two-way blocked design ANOVAs to test the effect of technique (burrow and visual) and month (May to November) on total, adult, and juvenile *U. pugnax* density. Technique and month were treated as fixed variables in analysis and plots were treated as a random effect. All data were square root transformed for analysis. Data were normally distributed (according to a Shapiro-Wilk test) and had equal variances (according to Levene tests) after transformation. Linear regression was used to test for a significant relationship between burrow and visual estimates of total density in August, September, and November of 2007. All analyses were run using JMP™ software.

To compare the efficiency of burrow, visual, and single excavation surveys for estimating total, adult, and juvenile *U. pugnax* density, data from the non-invasive surveys described above were compared with single excavation surveys. In order to compare techniques conducted on different plots, burrow estimates included only odd numbered plots (n=23) and visual estimates included only even numbered plots (n=22). Data for all three techniques were collected from July to November 2007 (excluding October). Single excavation surveys were conducted with 15 crab traps assembled from plastic chemical drums (described above; Figure 4). I haphazardly tossed these traps and then hammered them into the substrate at high tide each month. Once the tide receded, I counted, measured, and released all crabs that could be picked up off the surface; then, used a garden knife to excavate the substrate to about 10 cm, enumerating the remaining individuals.

To compare the efficiency of visual and single excavation surveys for estimating adult male and female *U. pugnax* densities, visual survey data from even numbered plots (n=22) described above were compared to estimates from single excavation surveys (n=15). Data included the months of July to November 2007 (excluding October). In visual surveys, males could only be distinguished from females by the presence of an enlarged cheliped, but in single excavation surveys, the shape of the abdomen could distinguish males that were missing a cheliped.

I conducted one-way, model-I ANOVAs to test the effect of technique (burrow, visual, and single excavation) on total, adult, and juvenile *U. pugnax* density (ind./m^2) for each month separately. I conducted one-way model-I ANOVAs to test the effect of technique (visual and single excavation) on male and female *U. pugnax* density (ind./m^2) for each month separately. I conducted Post-hoc Tukey tests to show differences between techniques within each month. I square root transformed all data and in all but a few cases, assumptions of parametric tests were satisfied. All analyses were run using JMP™ software.

II. Sampling effort, time efficiency, and precision

Finally, I compared non-invasive and invasive survey techniques according to cost and variance. For each technique, I roughly estimated the number of days spent in the field per month and the time invested in establishing individual plots. I also estimated the time invested in surveying individual plots each month. I added the financial cost associated with each survey technique, including equipment and travel funds.

Coefficients of variation (CV=SD / mean X 100) were calculated for burrow, visual, and single excavation surveys using total densities from the three-technique comparison (see section I-c). Coefficients of variation also were calculated for repeated excavation in both December 2007 and April 2008 and averaged.

RESULTS

I. Comparing the efficiency of survey techniques for estimating crab density.

(a) Comparing non-invasive (burrow and visual) and invasive (single and repeated excavation) survey techniques

There were significant differences in total density among survey techniques (df=3, 87; F=283.2; P<.0001; Table 1). Repeated excavation estimates were significantly higher than all other techniques, followed by burrow estimates (Figures 5 and 6). Single excavation and visual surveys were significantly lower than burrow surveys in both months, although single excavation estimated significantly higher density than visual in April 2008. Burrow and repeated excavation estimates of adult density were not significantly different. Only single and repeated excavation estimated more juveniles than adults (Figures 5 and 6). According to excavation surveys, juveniles (<9mm in width) composed, on average, about 70% of the population throughout the study. The most dominant size class measured 2.5 to 5mm in carapace width (Figure 7).

Total density varied significantly between months (df=1, 84; F=55.9; P<.0001). Repeated excavation estimates of juvenile density increased from 84.9 in December 2007 to 129.2 in April 2008, while estimates of adult density did not vary significantly among months (df=1,87; F=2.1; P=0.16; Table 1; Figures 5 and 6). There were no significant differences in burrow or visual estimates between months; however, single excavation enumerated more individuals in April 2008 than in December 2007.

There was no significant difference in total density among sampling days (df=3, 84; F=4.8; P=0.0038; Table 2). While estimates of adult males and females did vary significantly among days (df=3, 84; F=20.3 and 12.5 respectively; P<.0001 in both cases), estimates of juvenile density did not (df=3, 84; $F=2.0$; $P=0.12$). There was a significant interaction between sampling day and month for juvenile density (df=3,84; $F=28.6$; $P<.0001$; Table 2), which was due to increasing density with sampling day in December and decreasing density with sampling day in April. Twenty-eight percent of juveniles were captured on the first two sampling days in December 2007 whereas 65 percent were captured on days 1 and 2 in April 2008 (Figure 8). However, the percentage of adults captured decreased with sampling day in both months.

(b) Comparing non-invasive (burrow and visual) and single excavation survey techniques

Technique had the greatest effect on density, followed by month ($P<.0001$ in all cases, Table 3). Burrow surveys consistently yielded higher densities than visual surveys; however, only visual surveys suggested a clear pattern of change in abundance over time (Figures 9, 10, and 11). This pattern was characterized by a rise in crab density until August, then a sharp drop in crab density during fall. Linear regression analyses revealed a strong positive relationship between burrow and visual estimates of total density in August, September, and November of 2007 ($R^2=0.31$ $P<.0001$; $R^2=0.28$, $P=0.0002$; $R^2=0.25$, $P=0.0005$ respectively, Table 4 and Figure 12).

There were significant differences in density measured using burrow, visual, and single excavation survey methods in all 4 months (Tables 5, 6, and 7). Most of the variation was in the density of juveniles rather than adults (Tables 6 and 7). In July and August, significantly higher total density was measured using single excavation, followed by burrow and visual surveys respectively (Figure 13). This same pattern was true for juvenile density in all but November (Figure 14), but only true for adult density in July (Figure 15). In August and September, burrow and excavation estimates of adults were not significantly different. Only in November did burrow estimations of total, adult, or juvenile density exceed that of excavation.

Excavation estimates of male density were significantly higher than that of visual estimates in July and September, but not significantly different in August and November (Table 8, Figure 16). Excavation estimates of female density were significantly higher than visual estimates in all but November (Table 9, Figure 17).

II. Sampling effort, time efficiency, and precision

Invasive techniques were more costly than non-invasive methods (Table 10). A total of 6 days were spent in the field each month for the execution of invasive techniques, compared to only 1 day per month for non-invasive techniques. More time was spent on each plot for invasive techniques (15 to 60 min.) than for non-invasive techniques (1 to 3 min.). The cost of equipment and travel expenses was higher for invasive techniques. However, the coefficient of variation was lowest for repeated excavation (19.3), followed by burrow (32.8). Surprisingly visual and single excavation had very high coefficients of variation.

DISCUSSION

In previous comparisons of *Uca* survey techniques, burrow surveys estimated higher density than substrate excavation (Macia et al. 2001; Skov and Hartnoll 2001); however, in the present study, excavations, both single and repeated, enumerated more individuals than burrow surveys. While estimates of adult density were comparable between burrow and excavation surveys, estimates of juveniles were much higher in excavation surveys, particularly when plots were repeatedly excavated for 4 days. In December, 89% of juveniles were captured after the first sampling day with repeated excavations. The greatest difference among the techniques was the unique ability of excavations to accurately survey small juveniles (< 5 mm in width), which was the dominant size class in the population. In contrast, burrow and visual surveys estimated about twice as many adults as juveniles. Visual surveys consistently underestimated density when compared to other techniques, just as in previous survey comparisons in mangroves (Lourenco et al. 2000, Skov and Hartnoll 2001); however, visual estimates of density were highly correlated with that of burrow surveys, which may allow the researcher to calculate burrow densities with visual estimates using a linear equation. Despite their accuracy, invasive survey techniques were more costly than non-invasive techniques. Repeated excavation, however, provided more precise measurements of density than any other technique.

Repeated excavation provided accurate estimates of both adult and juvenile density, distinguished species and sex of trapped crabs, gave reliable estimates of size frequency distribution in the population, and carried the highest precision (Table 11). Only in November and December did single excavation yield unreliable density, a problem solved by repeated excavation. Eighty-nine percent of juveniles in December were collected after the first excavation, particularly small individuals measuring less than 5 mm in width. Use of repeated excavation may be completely necessary if one wishes to properly assess the dynamics or forecast the future of an Ocypodid population. Despite advantages in accuracy and precision, substrate excavation has many disadvantages. Excavation plots were time consuming, costing 12 min. to establish and up to 60 min. to survey, while non-invasive plots required only 1 min. to establish and up to 3 min. to survey (Table 11). As a result, far fewer plots could be surveyed with invasive techniques. Excavation cost more money to execute and required more trips to the marsh to complete, resulting in a higher cost of fuel. Excavation also requires that the observer wade out in up to 3 feet of water at high tide to set the traps, which may be unappealing to some. Perhaps the most undesirable aspect of excavation is the long-term damage to the habitat. Root systems destroyed during excavation may take several months to grow back, which many find unacceptable.

Burrow enumeration surveys offered reliable estimates of adults and bore the lowest cost (Table 11). The variation calculated for burrow counts was lower than that of visual or single excavation. I was able to sample more plots with burrow surveys because each plot only required a minute to count. This technique required only one field trip per month and cost only a few dollars for materials. The accuracy of burrow surveys is not affected by the time of day, tidal cycle, or lunar cycle, as are visual scanning and substrate excavation, which allows the observer more flexibility when planning field trips. However, there are disadvantages associated with the technique. Use of burrow quantification is largely based upon the belief that abandoned burrows fill in within weeks (Wolfrath 1992) which may not be the case, dependent on the depth of the burrow and root mat density. The presence of multiple species of burrowing crabs may cause overestimation of density, unless burrows are sufficiently distinct (Table 11). In the Tybee Island site, there was very little overlap in zones of *U. pugilator* and *U. pugnax*, but *Sesarma spp*. and juvenile *U. pugnax* burrows could be easily confused (personal observation). The same was true for juvenile *Panopeus spp.* burrows, which bore great resemblance to adult *U. pugnax* burrows. Particularly evident in this study was the underestimation of juveniles by burrow counting. Juvenile *U. pugnax* prefer to dig burrows on mounds associated with *Geukensia demissa* and stalks of *Spartina alterniflora*, which results in a patchy distribution of burrows (personal observation). These mounds were purposely avoided when distributing plots. As well, small burrows can also be difficult to see if pools of murky water are present in survey plots (personal observation). Use of burrow surveys must take such concerns into consideration.

Visual surveys offer some advantages over burrow and excavation techniques. While burrow enumeration cannot distinguish species or sex, visual surveying can. Visual surveys essentially offer a measure of surface activity, which has important biological implications (Table 11). For instance, males are known to synchronize their activity with that of the female reproductive cycle, which is highly influenced by the phase of the moon (Wheeler 1978; Greenspan 1982). Female surface activity remained low throughout the study, which may be due to increased risk of predation, as many birds prefer females over males (Iribarne and Martinez 1999; Ribeiro et al. 2003). Despite these advantages, visual surveys significantly underestimate both adult and juvenile density, which is likely due to the difficulty of spotting crabs at a distance in thick vegetation (Table 11), as evident in comparison studies in mangrove forests (Macia et al. 2001; Skov and Hartnoll 2001). Small juveniles (< 5mm) are especially difficult to spot at a distance (personal observation). Furthermore, individual crabs may be constantly moving during the observation time, either to avoid the observer or to forage at a different location. Counting mobile individuals from a distance may not, therefore, be a reliable estimate of density. Furthermore, the accuracy of this technique is highly dependant upon the time of day and the phase of the moon as *Uca spp*. activity is regulated by diurnal, tidal, and lunar rhythms (Webb and Brown 1965).

Each of these techniques can be useful in the context of a particular question. For instance, if a manager wishes to sustain a population of Ruddy Turnstones (*Arenaria interpres*), which are known to feed upon surface active males in some habitats (Iribarne and Martinez 1999), visually surveying crabs with binoculars may be appropriate, provided the vegetation is not too thick. However, if Whimbrels (*Numenius phaeopus*), which feed on burrowed females in certain regions (Iribarne and Martinez 1999), are the bird of interest, then excavation surveys may be the best choice. Burrow enumeration may be appropriate when adult density is of interest or when the effect of *Uca* burrows on vegetative production is in question. When considering the overall health and future of a fiddler crab population, only repeated excavation may offer reliable estimates of juvenile density.

Based upon my research, burrow surveys offer future researchers the best benefits in terms of accurate adult *Uca spp*. density and the ease and affordability with which it can be executed. However, if he needs accurate juvenile density or the study requires size frequency distribution, I recommend the use of repeated excavation. In addition, the trap design I used is cheap to construct and durable against the elements. Visual surveys should be used with caution, especially in habitats with dense vegetation. If a researcher needs a fast and easy measure of male and female density, visual surveys can be used, then converted to burrow estimates using one of the linear equations developed in my study.

In future, comparisons should be made on multiple sites to test whether differences in the density of vegetation or in the composition of the animal community affect the accuracy of each survey technique. Future studies could also survey multiple species, which may illuminate optimal techniques for certain crabs. The trapping technique developed in this study should be tested in mangrove forests to examine the practicality of hammering these traps into areas with thick tree roots. Although marsh substrate is difficult to sieve, future research may develop a more effective method for doing so, such as the use of machinery to better separate the roots. Such a method may allow all trapped crabs to be surveyed in a single excavation. Furthermore, the relationship between predators and fiddler population dynamics could be studied using multiple survey techniques. For instance, plots could be surveyed with multiple methods both before and after a flock of avian predators forages.

Fiddler crabs play an invaluable role in estuarine ecosystems, providing an important link by consuming algae and organic debris and providing a source of food for countless animals. According to repeated excavation surveys, Tybee Island has over a billion fiddler crabs in its 1800 acres of marsh, of which over 970 million are juveniles. This constitutes a major source of food on the island for resident and migratory birds, mammals, fish, and other species of crabs. The preservation of such a large population requires accurate and practical survey techniques that are versatile enough to be useful in various habitats and during different seasons. For instance, the impact of a violent storm on the marsh ecosystem would not be complete without an accurate measure of *Uca spp*. density both before and after the event. Nor can we foresee the future of dependent predator populations, such as the Whimbrel, until we have a reliable estimate of fiddler crab density. As a result of monitoring *Uca* populations, we can preserve salt marshes and mangrove forests, which are known to be some of the most productive and important ecosystems on earth.

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Table 1. Variation in total, adult, and juvenile *Uca pugnax* densities (ind./m^2) among survey techniques and months. Techniques include burrow, visual, single excavation, and repeated excavation. Surveys were conducted in December 2007 and again in April 2008. Data were square root transformed for analysis.

Source	DF	SS	MS	F-ratio	Prob > F
(a) Total					
Technique	3	938.2	312.7	176.2	<.0001
Month	1	65.0	65.0	55.9	<.0001
Plot [Month]	28	32.5	1.2		
Error	87	154.4	1.8		
Total	119	1190.0			
(b) Adult					
Technique	3	201.9	67.3	90.3	<.0001
Month	1	3.2	3.2	2.1	0.1622
Plot [Month]	28	43.6	1.6		
Error	87	64.8	0.7		
Total	119	313.5			
(c) Juveniles					
Technique	3	893.2	297.7	154.1	<.0001
Month	1	92.7	92.7	70.9	<.0001
Plot [Month]	28	36.6	1.3		
Error	87	168.1	2.0		
Total	119	1190.6			

Table 2. Variation in total, male, female, and juvenile *Uca pugnax* densities (ind./m^2) measured by repeated excavation among sampling days and months. Plots were excavated for 4 consecutive days during each visit. Surveys were conducted in December 2007 and again in April 2008. Data were square root transformed for analysis.

Source	DF	SS	MS	F-ratio	Prob > F
(a) Total					
Day	3	26.2	8.7	4.8	0.0038
Month	1	28.2	28.2	17.3	0.0003
Day*Month	3	128.6	42.9	23.6	<.0001
Plot [Month]	28	45.6	1.6		
Error	84	152.3	1.8		
Total	119	380.9			
(b) Male					
Day	3	73.3	24.4	20.3	<.0001
Month	1	1.8	1.8	1.9	0.1803
Day*Month	3	12.9	4.3	3.6	0.0177
Plot [Month]	28	26.4	0.9		
Error	84	101.3	1.2		
Total	119	215.7			
(b) Female					
Day	3	41.1	13.7	12.5	<.0001
Month	1	4.0	4.0	2.4	0.1308
Day*Month	3	17.5	5.8	5.3	0.0021
Plot [Month]	28	46.6	1.7		
Error	84	92.2	1.1		
Total	119	201.4			
(c) Juveniles					
Day	3	11.8	3.9	2.0	0.1179
Month	1	57.5	57.5	30.7	<.0001
Day*Month	3	167.7	55.9	28.6	<.0001
Plot [Month]	28	52.4	1.9		
Error	84	164.0	2.0		
Total	119	453.4			

Table 3. Variation in total, adult, and juvenile *Uca pugnax* densities (ind/m^2) among survey techniques and months. Techniques include burrow and visual surveys conducted on 45 permanent study plots during 6 months beginning in May 2007. Data were square root transformed for analysis.

Source	DF	SS	MS	F-ratio	Prob > F
(a) Total					
Technique	1	1428.4	1428.4	715.4	<.0001
Month	5	313.9	62.8	31.4	<.0001
Plot	44	484.5	11.0		
Error	489	976.4	2.0		
Total	539	3203.2			
(b) Adult					
Technique	1	725.6	725.6	542.5	<.0001
Month	5	157.4	31.5	23.5	<.0001
Plot	44	258.3	5.9		
Error	489	654.1	1.3		
Total	539	1795.4			
(c) Juvenile					
Technique	1	715.6	715.6	281.8	<.0001
Month	5	206.9	41.4	16.3	<.0001
Plot	44	458.9	10.4		
Error	489	1241.9	2.5		
Total	539	2623.4			

Table 4. Relationship between visual and burrow estimates of total *U. pugnax* density in August, September, and November of 2007.

Month	Formula	R^2	F	P
August	BUR= 1.1*VIS + 31.1	0.31	19.4	<.0001
September	BUR= 0.9*VIS + 32.3	0.28	17.0	0.0002
November	BUR= 1.2*VIS + 63.1	0.25	14.1	0.0005

Table 5. Variation in total *Uca pugnax* density (ind/m2) among survey techniques. Surveys were conducted during 4 months in 2007. Odd numbered plots were used for burrow surveys (n=23) and even numbered plots for visual surveys (n=22). Excavation surveys were conducted separately (n=15). Data were square root transformed for analysis.

Source	DF	SS	MS	F-ratio	Prob > F
(a) July					
Technique	2	375.5	187.7	111.8	<.0001
Error	56	94.0	1.7		
Total	58	469.5			
(b) August					
Technique	2	149.8	74.9	25.7	<.0001
Error	56	163.2	2.9		
Total	58	313.0			
(c) September					
Technique	2	102.9	51.4	18.4	<.0001
Error	57	158.9	2.8		
Total	59	261.8			
(d) November					
Technique	2	422.4	211.2	93.1	<.0001
Error	57	129.3	2.3		
Total	59	551.7			

Table 6. Variation in adult *Uca pugnax* density (ind/m2) among survey techniques. Surveys were conducted during 4 months in 2007. Odd numbered plots were used for burrow surveys (n=23) and even numbered plots for visual surveys (n=22). Excavation surveys were conducted separately (n=15). Data were square root transformed for analysis.

Source	DF	SS	MS	F-ratio	Prob > F
(a) July					
Technique	2	276.2	138.1	68.5	<.0001
Error	56	112.8	2.0		
Total	58	389.0			
(b) August					
Technique	2	173.2	86.6	26.4	<.0001
Error	56	183.9	3.3		
Total	58	357.1			
(c) September					
Technique	2	44.7	22.4	5.4	0.0071
Error	57	235.8	4.1		
Total	59	280.6			
(d) November					
Technique	2	345.0	172.5	59.0	<.0001
Error	57	166.7	2.9		
Total	59	511.7			

Table 7. Variation in juvenile *Uca pugnax* density (ind/m2) among survey techniques. Surveys were conducted during 4 months in 2007. Odd numbered plots were used for burrow surveys (n=23) and even numbered plots for visual surveys (n=22). Excavation surveys were conducted separately (n=15). Data were square root transformed for analysis.

Source	DF	SS	MS	F-ratio	Prob > F
(a) July					
Technique	2	110.9	55.5	26.7	<.0001
Error	56	116.5	2.1		
Total	58	227.4			
(b) August					
Technique	2	27.1	13.6	6.8	0.0023
Error	56	112.0	2.0		
Total	58	139.1			
(c) September					
Technique	2	80.1	40.1	26.5	<.0001
Error	57	86.2	1.5		
Total	59	166.3			
(d) November					
Technique	2	117.8	58.9	29.8	<.0001
Error	57	112.5	2.0		
Total	59	230.4			

Table 8. Variation in male *Uca pugnax* density (ind/m2) between survey techniques. Techniques include visual (n=22) and single excavation (n=15) surveys conducted during 4 months beginning in July 2007. Data were square root transformed for analysis.

Source	DF	SS	MS	F-ratio	Prob > F
(a) July					
Technique	1	67.7	67.7	46.8	<.0001
Error	34	49.2	1.4		
Total	35	116.9			
(b) August					
Technique	1	3.2	3.2	1.8	0.1840
Error	34	59.4	1.7		
Total	35	62.7			
(c) September					
Technique	1	46.1	46.1	36.3	<.0001
Error	35	44.5	1.3		
Total	36	90.6			
(d) November					
Technique	1	1.5	1.5	0.8	0.3865
Error	35	68.4	2.0		
Total	36	69.9			

Table 9. Variation in female *Uca pugnax* density (ind/m2) between survey techniques. Techniques include visual (n=22) and single excavation (n=15) surveys conducted during 4 months beginning in July 2007. Data were square root transformed for analysis.

Source	DF	SS	MS	F-ratio	Prob > F
(a) July					
Technique	1	41.1	41.1	18.7	0.0001
Error	34	74.5	2.2		
Total	35	115.6			
(b) August					
Technique	1	9.5	9.5	9.1	0.0047
Error	34	35.5	1.0		
Total	35	45.0			
(c) September					
Technique	1	10.5	10.5	8.5	0.0063
Error	35	43.3	1.2		
Total	36	53.8			
(d) November					
Technique	1	0.02	0.02	0.01	0.9114
Error	35	47.6	1.4		
Total	36	47.6			

Table 10. Cost and variance analysis for invasive (single excavation (SIN EXC) and repeated excavation (REP EXC)) and non-invasive (burrow (BUR) and visual (VIS)) fiddler crab survey techniques.

	Non-invasive		Invasive	
	BUR	VIS	SIN EXC	REP EXC
No. plots / month	45	45	15	15
Days in the field / month	1	1	2	4
Set-up time / plot (min)	1	1	12	12
Survey time / plot (min)	1	3	15	60
Equipment cost (US$) *	12	50-2000	160	160
Travel cost / month (US$)	20	20	40	80
Coefficient of Variation **	32.8	44.3	45.3	19.3

*Depends on cost of binoculars.
** CV = Standard Deviation ÷ Mean X 100 (expressed as average CV for all months)

Table 11. A summary of the advantages and disadvantages of burrow, visual, and excavation survey techniques.

Technique	Advantages	Disadvantages
Single and Repeated Excavation	Accurate estimates of adult and juvenile density Highest precision with repeated excavation	Time consuming Destroys habitat
Burrow surveys	Reliable estimates of adult density Fast, easy, and affordable	Difficult to distinguish species and sex
Visual surveys	Measure of surface activity Fast, easy, and affordable	Difficult to spot crabs at a distance in thick vegetation

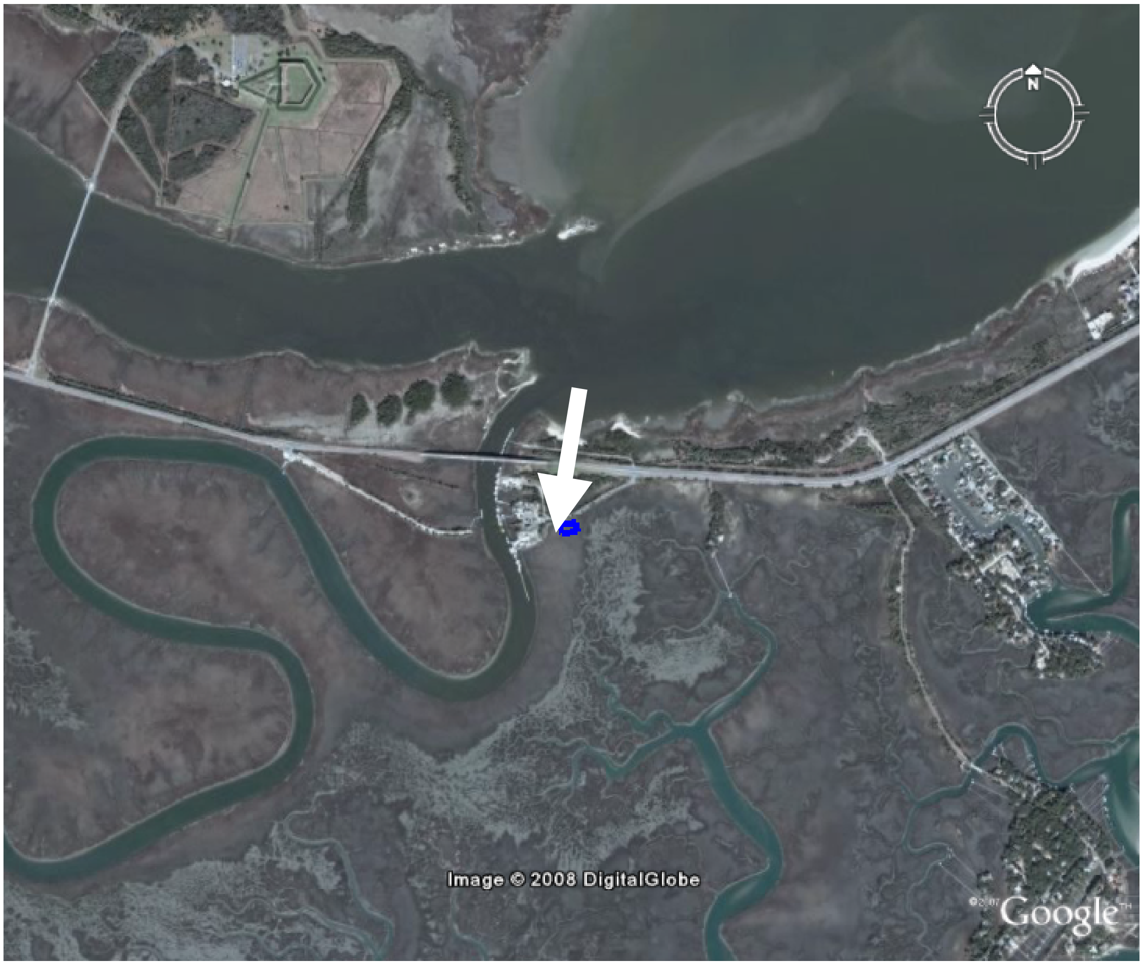

Figure 1. Study site on Tybee Island, Georgia (32°00'49N and 80°52'52W). The salt marsh is fed by Lazaretto Creek seen just to the west of the site. The white arrow indicates the location of the study site.

Figure 2. Photograph of study site on Tybee Island, Georgia.

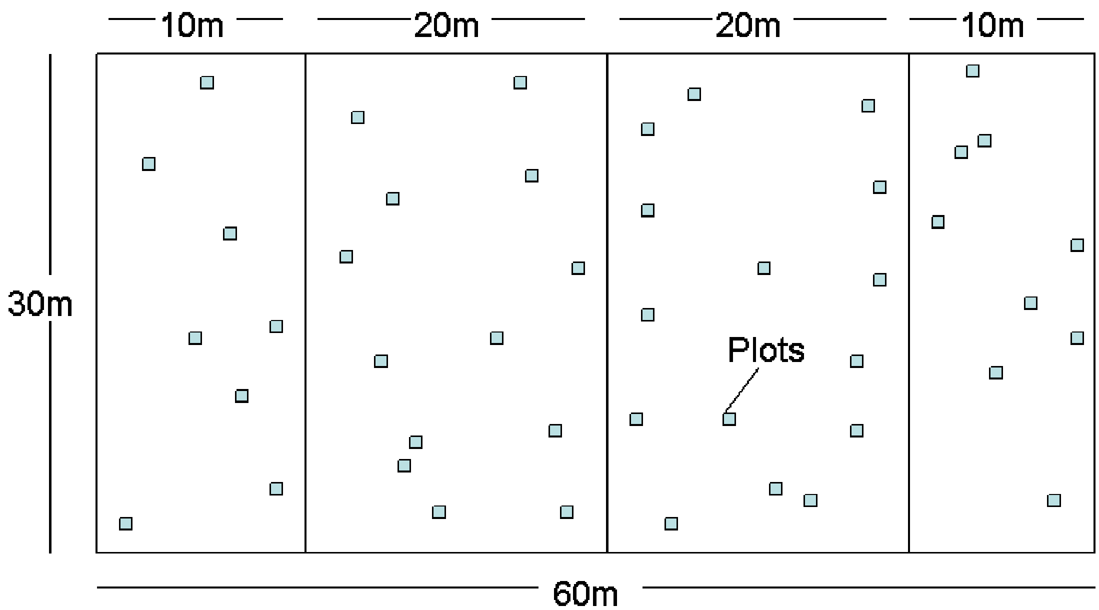

Figure 3: Sampling scheme for non-invasive and invasive survey techniques. Non-invasive surveys include 45 permanent plots distributed haphazardly on either side of three transect lines. Invasive surveys include 15 traps distributed haphazardly each month on either side of three transect lines. Transect lines were 20m apart and 30m long.

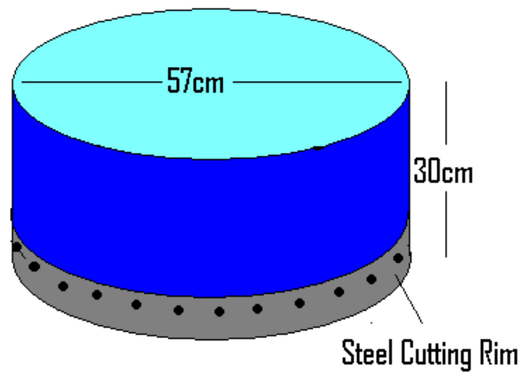

Figure 4. Cylindrical traps used in single and repeated excavation surveys. Traps were assembled from 208 L plastic chemical drums and had a steel strap fastened around the base for cutting through the substrate.

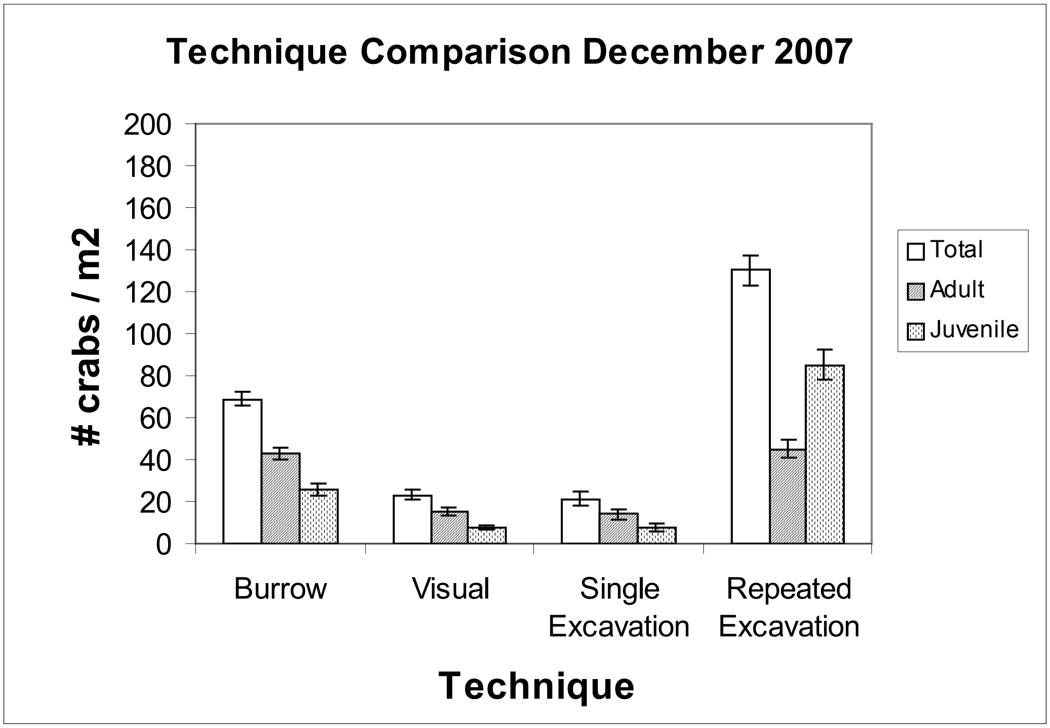

Figure 5. Mean (± 1 SE) total, adult, and juvenile *Uca pugnax* density (ind/m^2) measured using burrow, visual, single excavation, and repeated excavation survey methods in December 2007 (n=15).

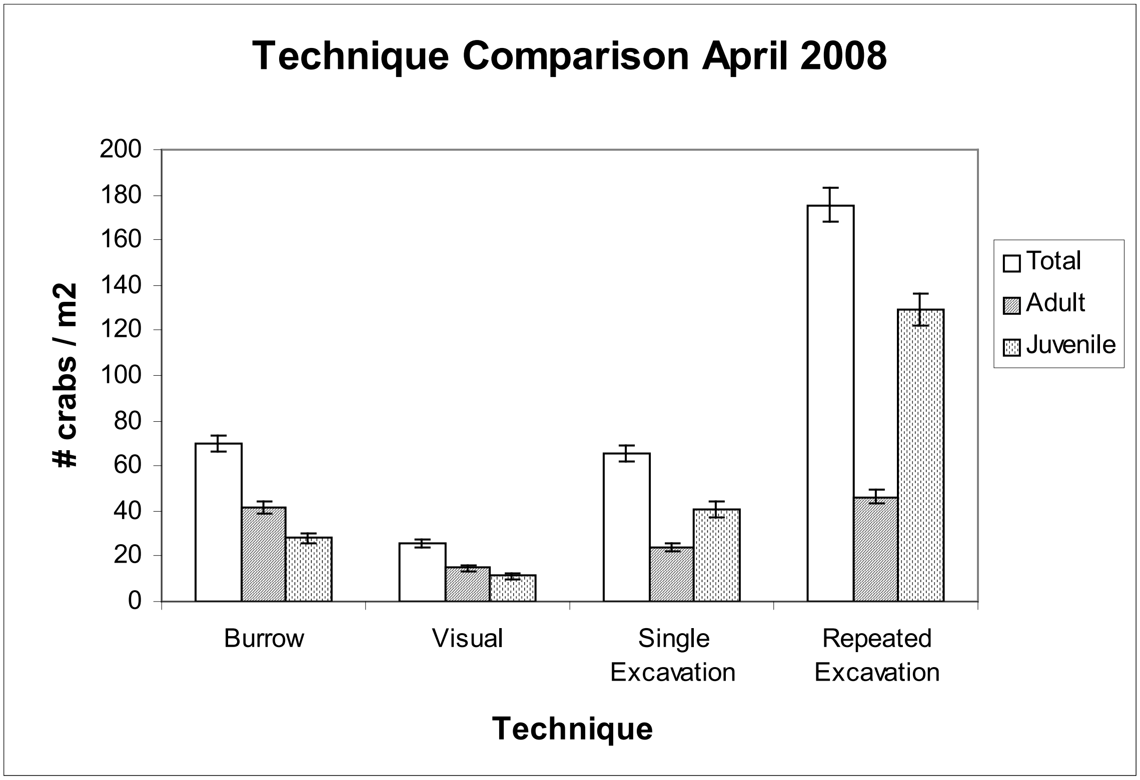

Figure 6. Mean (± 1 SE) total, adult, and juvenile *Uca pugnax* density (ind/m^2) measured using burrow, visual, single excavation, and repeated excavation survey methods in April 2008 (n=15).

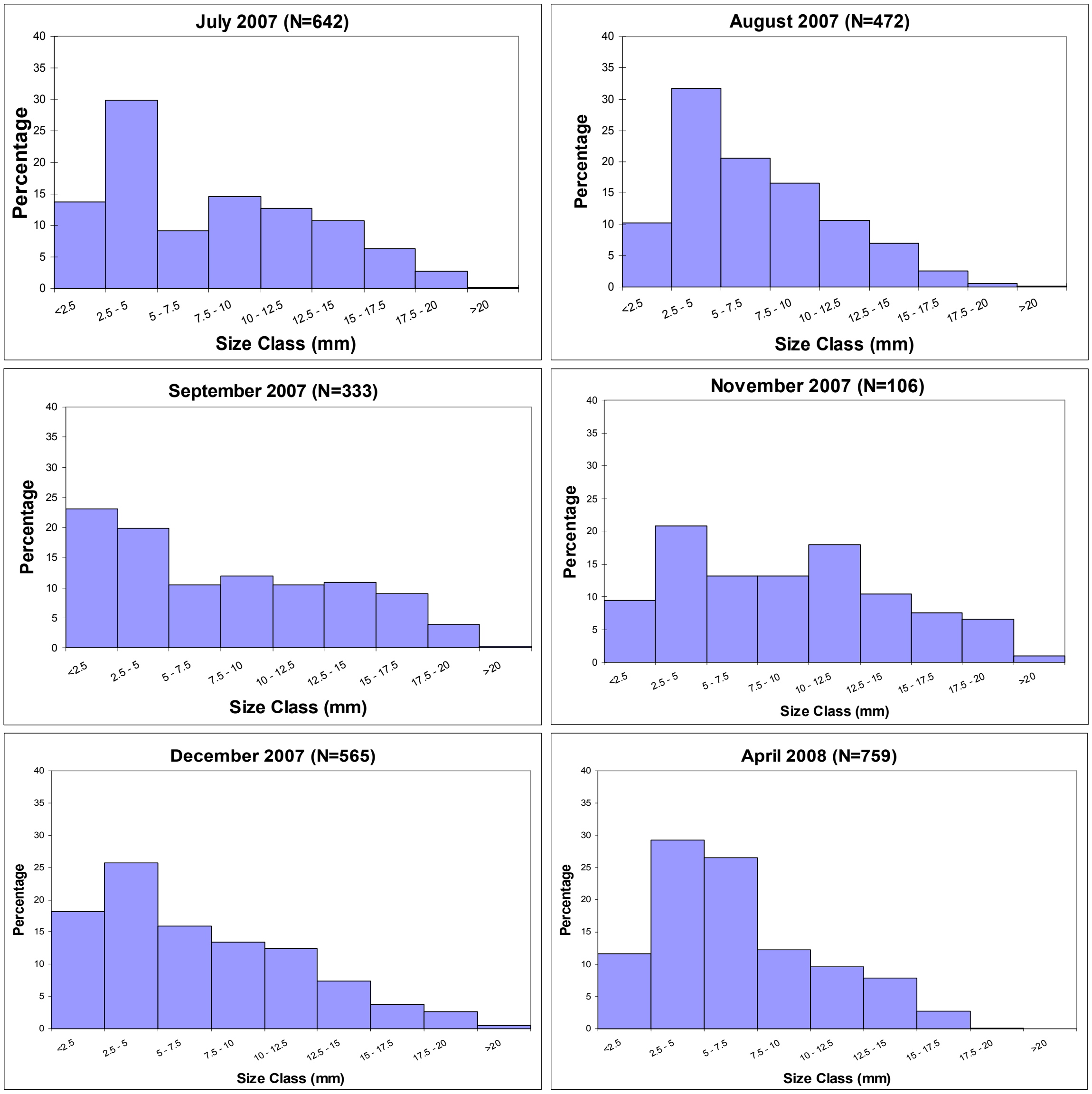

Figure 7. Size distribution histograms illustrating the percentage of *Uca pugnax* in each of 9 categories based on carapace width (mm). Crabs were measured as part of the excavation surveys conducted from July to December 2007.

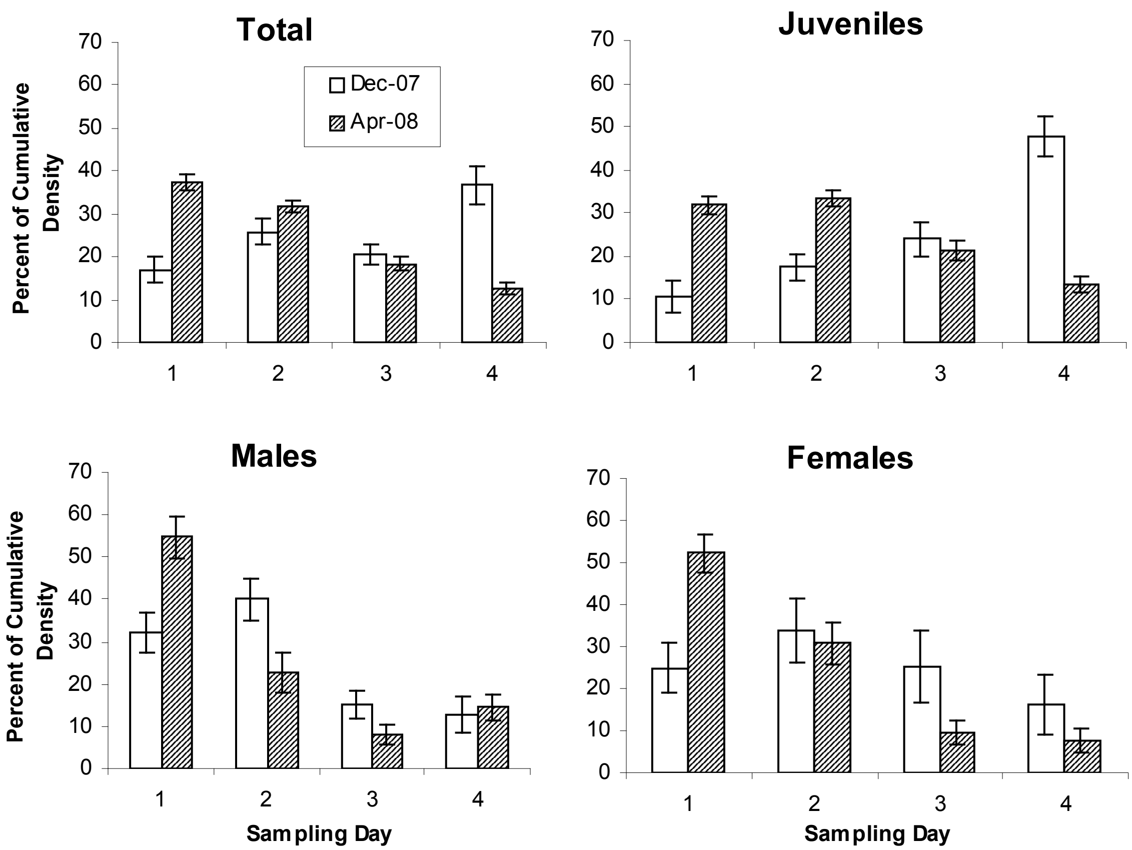

Figure 8. Percent of cumulative *Uca pugnax* density collected by repeated excavation on each sampling day (n=15). Data includes total, juvenile, male, and female densities measured in December 2007 and April 2008.

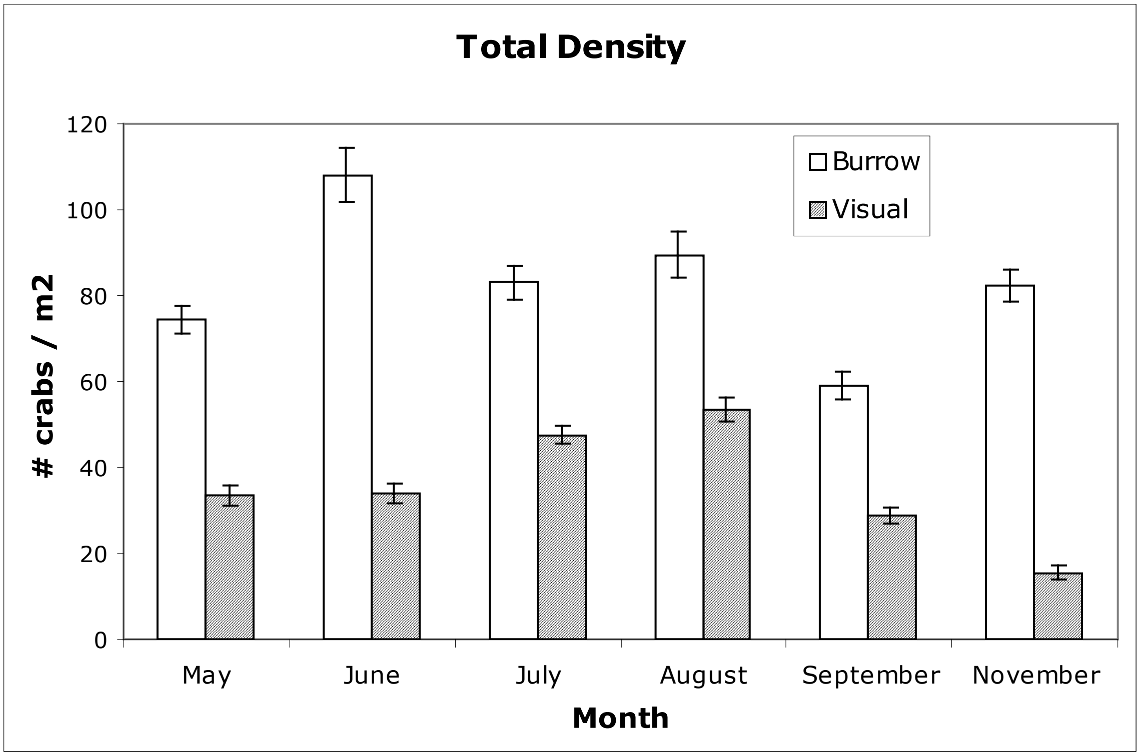

Figure 9. Mean (± 1 SE) total *Uca pugnax* density (ind/m^2) measured using burrow and visual survey techniques during six months in 2007 (n=45).

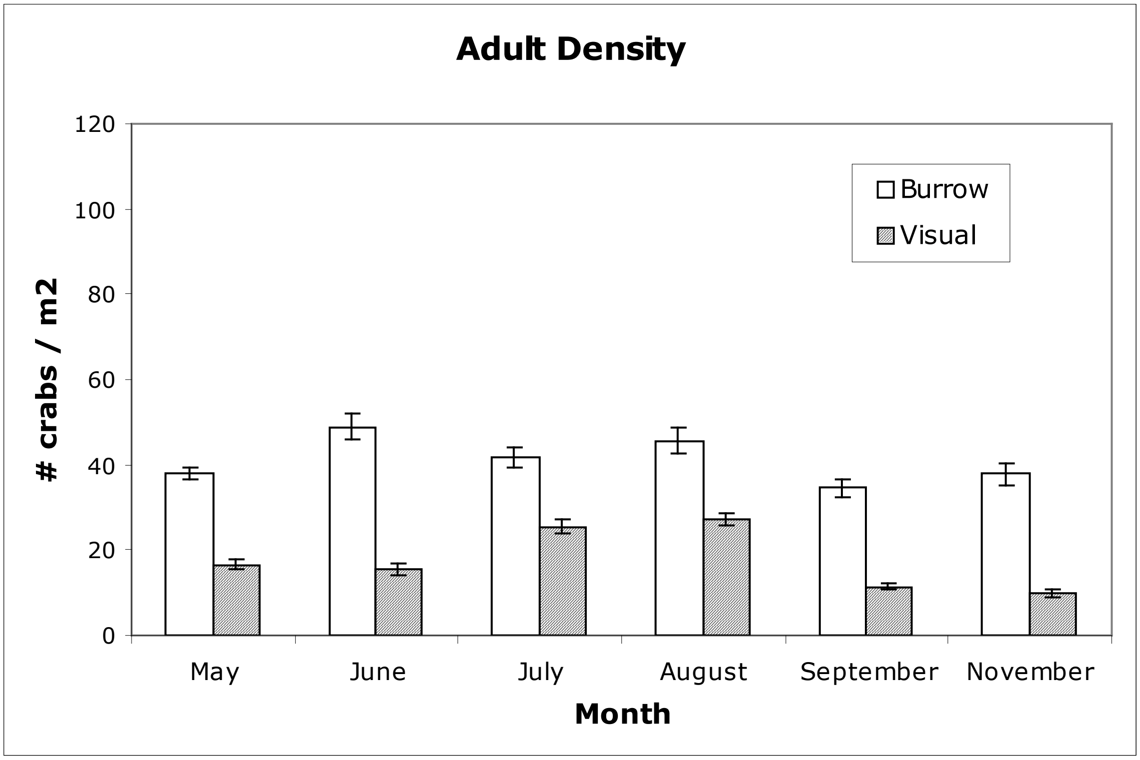

Figure 10. Mean (± 1 SE) adult *Uca pugnax* density (ind/m^2) measured using burrow and visual survey techniques during six months in 2007 (n=45).

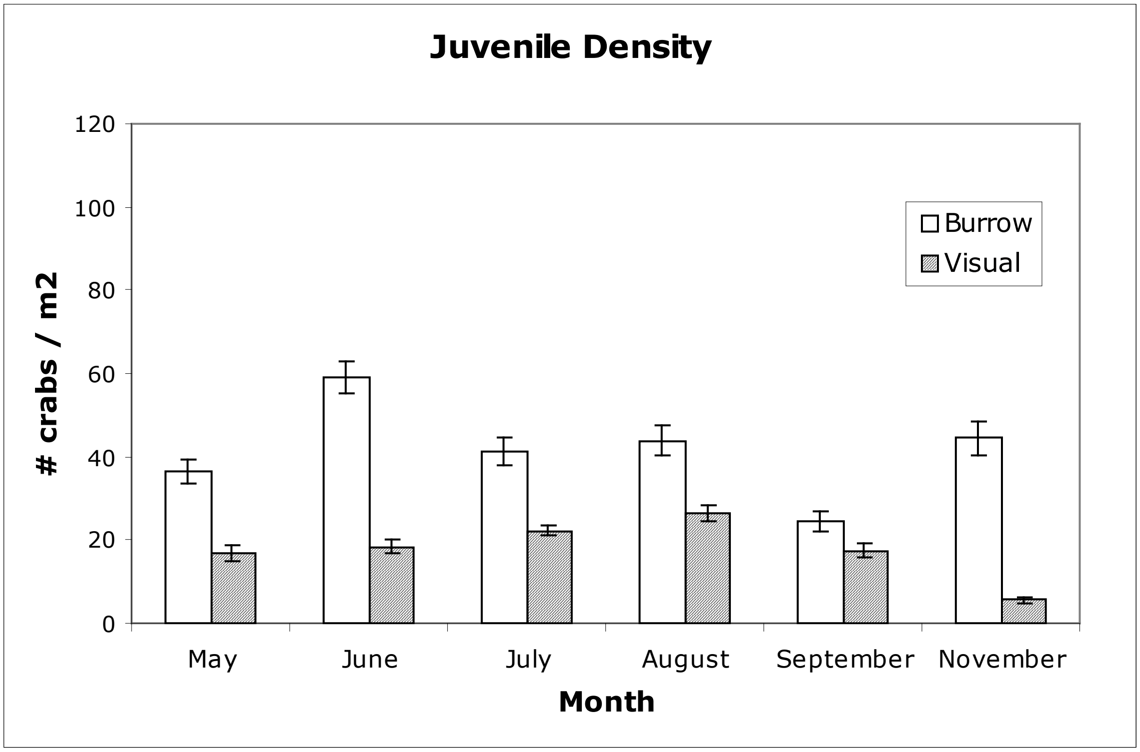

Figure 11. Mean (± 1 SE) juvenile *Uca pugnax* density (ind/m^2) measured using burrow and visual survey techniques during six months in 2007 (n=45).

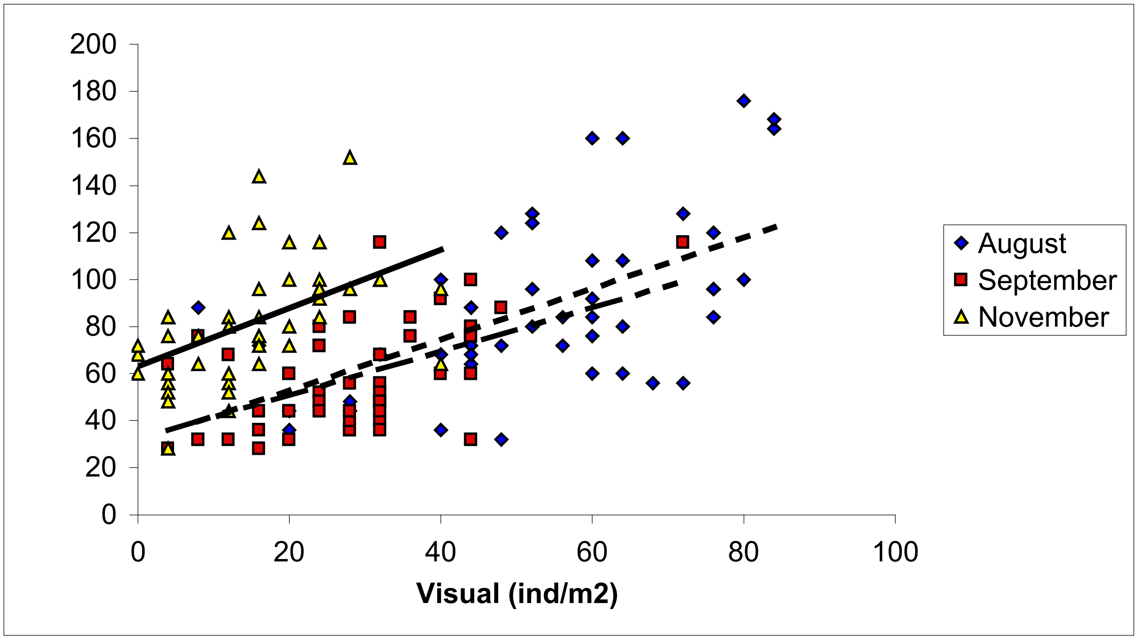

Figure 12. Relationship between visual and burrow estimates of total crab density (ind./m^2) for August, September, and November (R^2=0.31, 0.28, 0.25 respectively). Strong linear relationship allows the calculation of burrow surveys using visual estimates, but only when burrow counts are above 24 crabs per square meter.

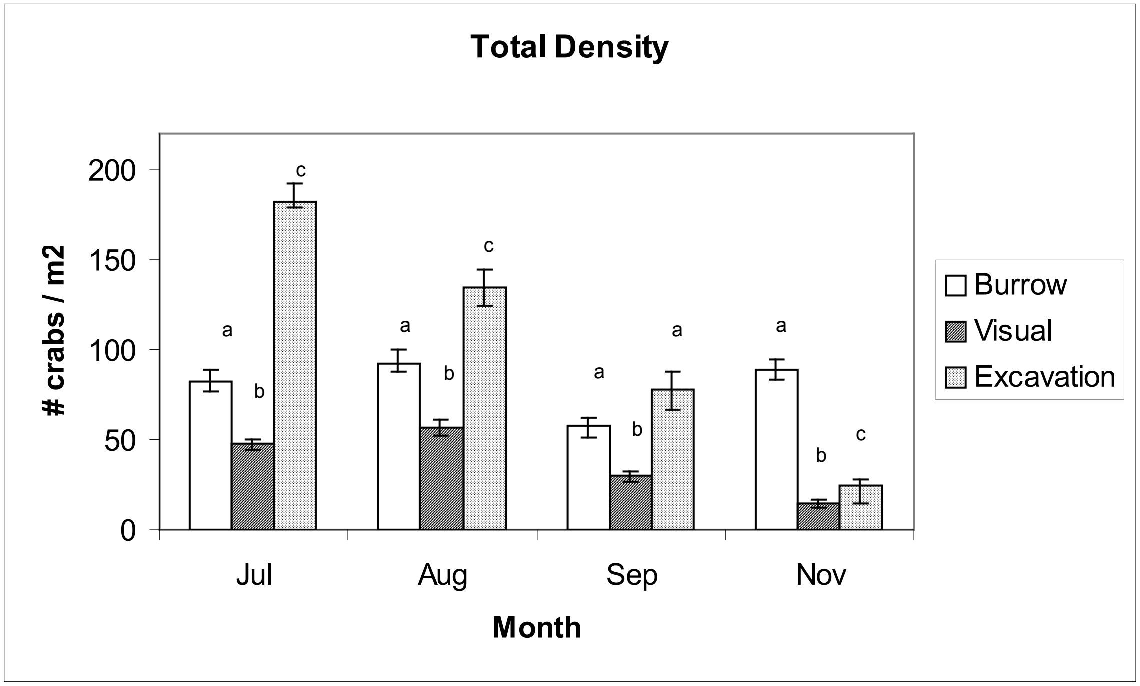

Figure 13. Mean (± 1 SE) total *Uca pugnax* density (ind./m^2) measured using burrow, visual, and single excavation survey methods conducted during 4 months beginning in July 2007. Different letters indicate significant differences from other techniques within individual months.

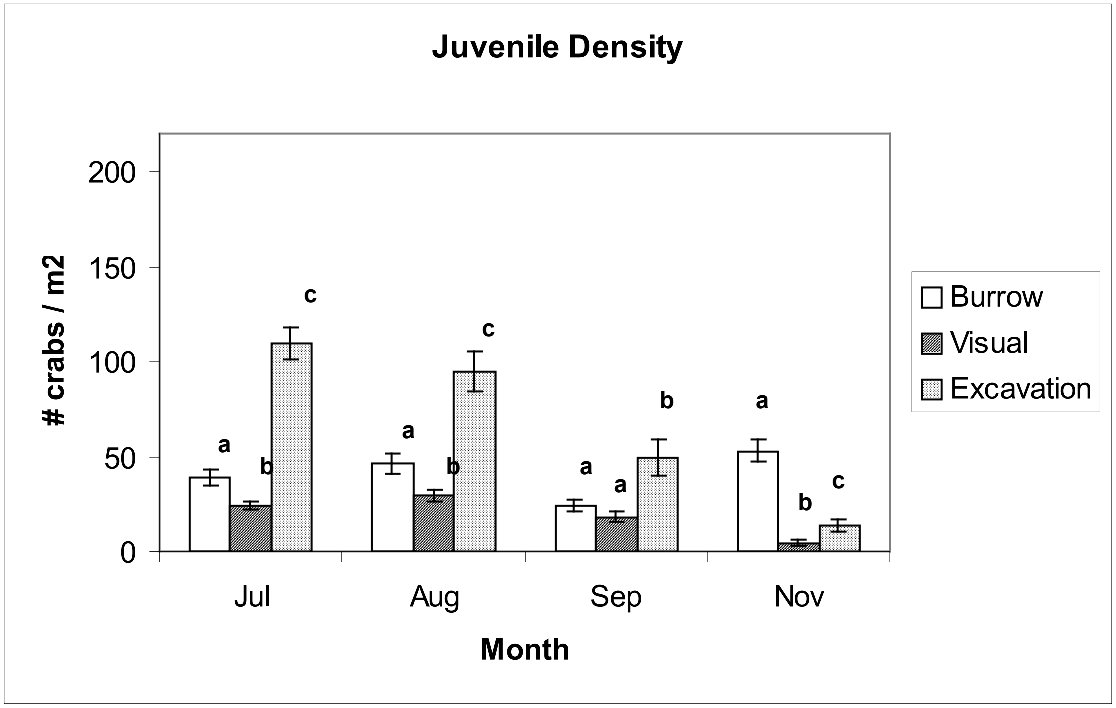

Figure 14. Mean (± 1 SE) juvenile *Uca pugnax* density (ind./m^2) measured using burrow, visual, and single excavation survey methods conducted during 4 months beginning in July 2007. Different letters indicate significant differences from other techniques within individual months.

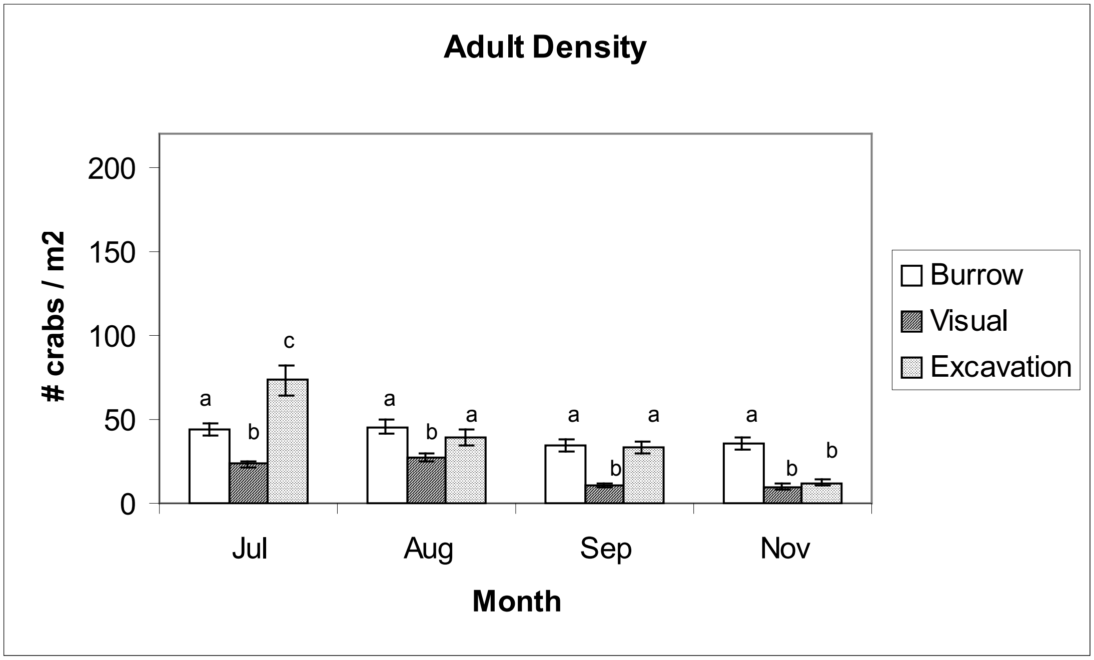

Figure 15. Mean (± 1 SE) adult *Uca pugnax* density (ind./m^2) measured using burrow, visual, and single excavation survey methods conducted during 4 months beginning in July 2007. Different letters indicate significant differences from other techniques within individual months.

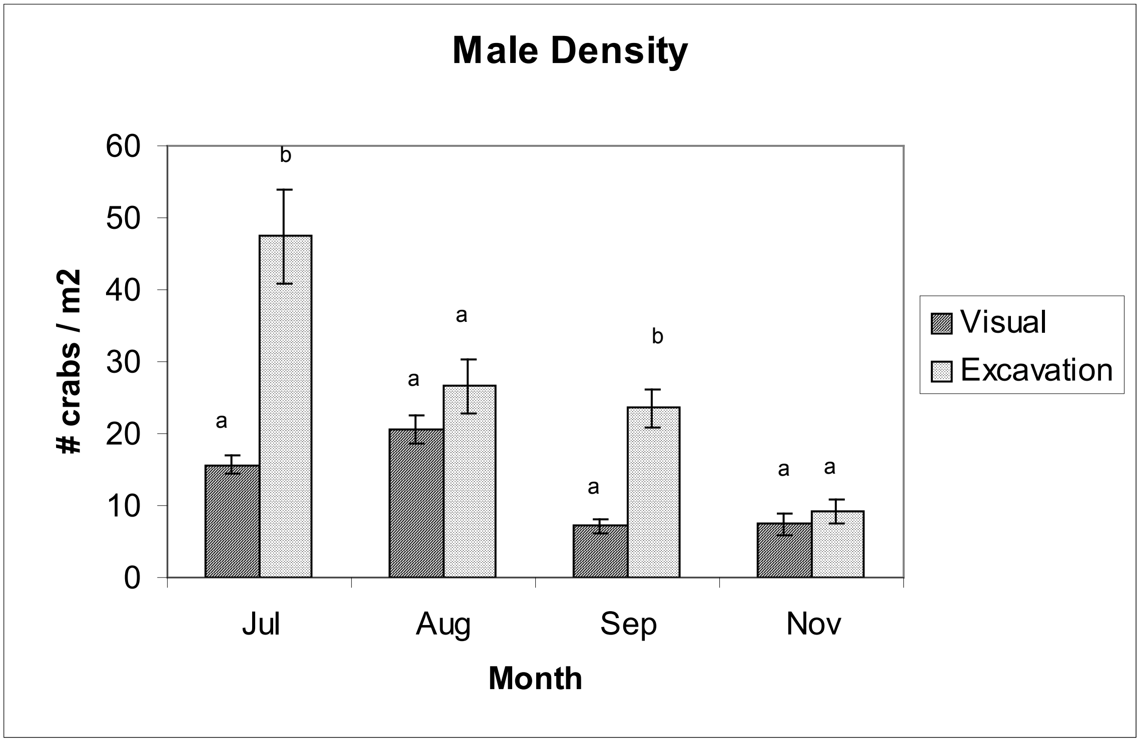

Figure 16. Mean (± 1 SE) male *Uca pugnax* density (ind./m^2) measured using visual and single excavation survey methods conducted during 4 months beginning in July 2007. Different letters indicate significant differences from other techniques within individual months.

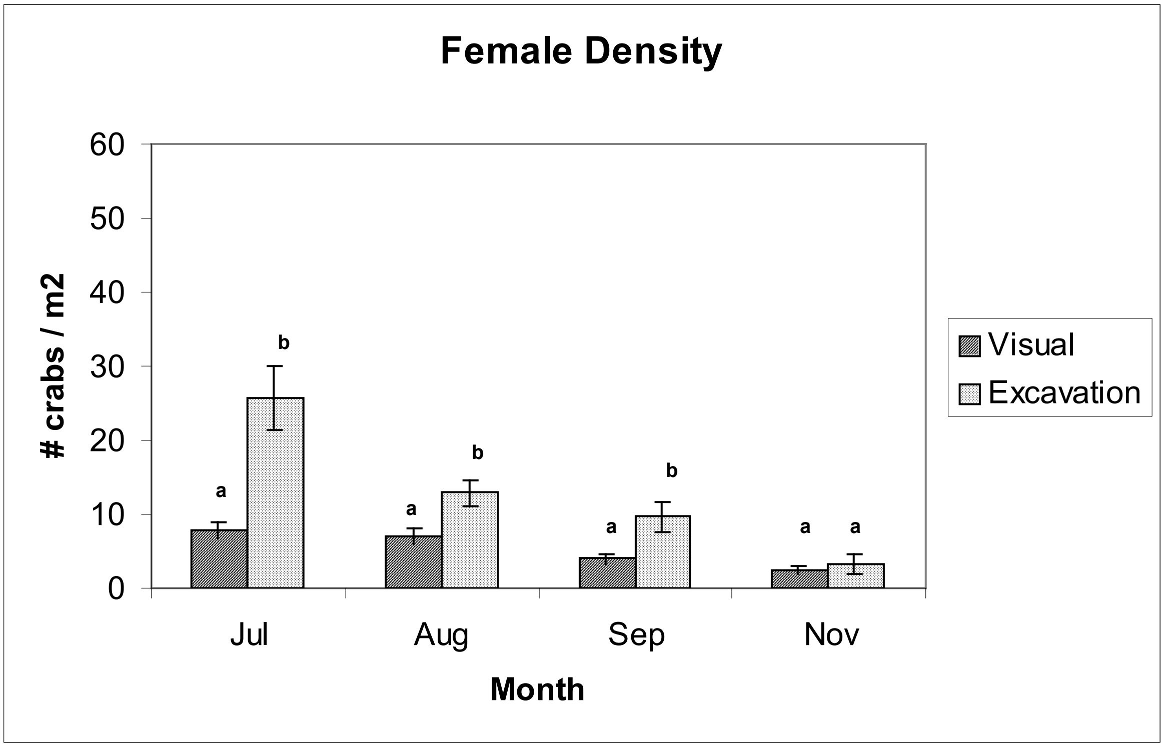

Figure 17. Mean (± 1 SE) female *Uca pugnax* density (ind./m^2) measured using visual and single excavation survey methods conducted during 4 months beginning in July 2007. Different letters indicate significant differences from other techniques within individual months.